

SYSTEMATICS AND BIOLOGY OF THE SOUTHERN WESTERN AUSTRALIAN CENTROLEPIDACEAE

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ABSTRACT

The Centrolepidaceae are a small Family of 33 species distributed in four genera *Aphelia*, *Brizula*, *Centrolepis* and *Gaimardia*. The genera *Hydatella* and *Trithuria* were until recently also considered members of this family, but are now placed in a segregate family, the Hydatellaceae.

Members of the two families differ markedly in their biology. Members of the Hydatellaceae are true submerged aquatics (usually ephemeral in life history), whereas the Centrolepidaceae are wetland or terrestrial plants. Dioecy and unisexual inflorescences are common in the Hydatellaceae and not in Centrolepidaceae. Seed dispersal is often by seeds being held on the plant by Centrolepidaceae but liberated by Hydatellaceae. Apomixis and obligate outbreeding occurs in Hydatellaceae, modal outbreeding, inbreeding/self fertility are found in the Centrolepidaceae. Many of the distinguishing characters between the families are related to these differences in basic biology.

Recently the genera *Aphelia* and *Brizula* have again been merged but inflorescence structure strongly suggests that these genera should remain separate.

In terms of its members' biology and morphology the family has little in common with the Jointed Sedges (Restionaceae).

INTRODUCTION

The Centrolepidaceae are a small Family of 33 species distributed in four genera: *Aphelia*, *Brizula*, *Centrolepis* and *Gaimardia*. The genera *Hydatella* and *Trithuria* were until recently also considered members of this family, but were segregated as the family Hydatellaceae by Hamann

(1976). Dahlgren *et al.* (1985) has usually placed these families in a group of families with the Jointed Sedges (Restionaceae) and more distantly the Grasses (Poaceae). This paper contrasts aspects of the biology of these related families.

Members of the family Centrolepidaceae are largely

confined to the Southern Hemisphere and are thought to be Gondwanan in origin and present distribution, although one species extends through South East Asia to Laos. Centres of diversity are South Western Australia and Tasmania (Cooke 1983). Cooke (1980,1986, 1992 and 1995) has elucidated the taxonomy of the largest genera, *Centrolepis* and *Aphelia* (including *Brizula*).

Both *Centrolepidaceae* and *Hydatellaceae* have been very poorly collected and understood, especially in the major centre of diversity, Western Australia. For example, Marchant and Keighery (1979) listed 6 species with no collections in PERTH and 4 others with less than 5 collections in the first attempt to list rare species in the Western Australian flora. They were unable to determine the conservation status of any member of both families. This paper attempts to summarise what is known about the biology of members of the family *Centrolepidaceae*.

MATERIALS AND METHODS

Most of the information presented here is the result of extensive collecting of the family and studies of live plants undertaken while the author was research botanist at Kings Park and Botanic Garden. The isoflor map (Figure 1) summarises the known distributions of all 20 taxa plotted within a one degree

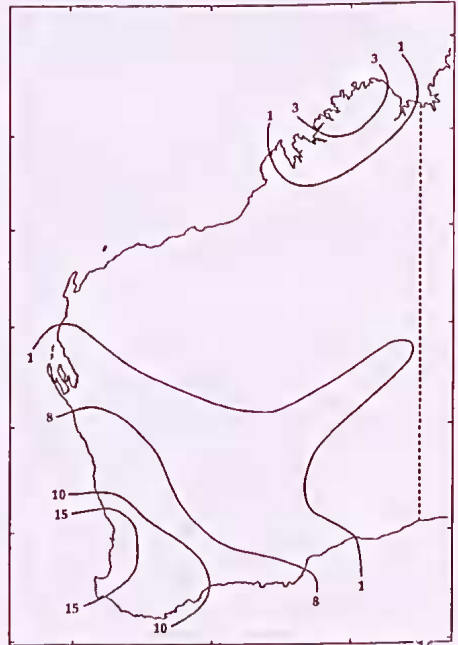


Figure 1. Isoflor map of Western Australian *Centrolepidaceae* showing relative species richness of areas.

grid, the number of species within each square counted and isoflors drawn to connect areas of equal species richness.

COMPOSITION AND PHYTOGEOGRAPHY

The Western Australian *Centrolepidaceae* comprise the monotypic genus *Aphelia*, three species of *Brizula* and 16 taxa of *Centrolepis*. There are also three species (*Centrolepis banksii*, *C. curta* and *C. exserta*) in tropical Western Australia, but this paper will only deal with the extra-tropical species. Of these, the genus *Aphelia*, and 13 other taxa

(65%) are endemic to the region. This figure is comparable to other major groups present and species diverse in southern Western Australia, such as the Myrtaceae (68% of taxa endemic) or the Proteaceae (74%), Keighery (1996).

Species endemism is probably lower than the other major groups of species diverse Monocotyledons (Anthericaceae, Cyperaceae, Haemodoraceae and Restionaceae) in southern Western Australia (Keighery 1984). These groups have been able to colonize the dry nutrient poor soils of the area and are thus species diverse on the northern and southern sandplains, producing numerous localised endemics (Johnson and Briggs 1981).

However, Southern Western Australia is a centre of diversity for the Centrolepidaceae, as it is for the Hydatellaceae, which has two genera, *Hydatella* (3 described species, with potentially 2 undescribed) and *Trithuria* (2 species) in southern Western Australia. The family has 6 endemic species of the 7 recorded for southern Western Australia (84% endemism).

Most members of the family Centrolepidaceae and Hydatellaceae are confined to temperate Western Australia (Figures 1 and 2). Four species (*Centrolepis eremica*, *C. cephaloformis*, *C. humillima* and *C. polygyna*) extend into the arid zone. These species have all been able to occupy microhabitats



Figure 2. Isoflor map of Western Australian Hydatellaceae showing relative species richness of areas.

within the large saltlake palaeodrainage systems present in this area. These taxa all also occur in Eastern Australia. Hydatellaceae (Figure 2) in southern Western Australia are confined to the coastal higher rainfall areas and are apparently most diverse on the claypans of the Swan Coastal Plain, but this may reflect sampling intensity (Gibson *et al.* 1994).

While many taxa are still undercollected, it would appear that all species of Centrolepidaceae are relatively widespread and present in numerous conservation reserves in the region. This is quite at variance with the Restionaceae,

Table 1. Biological Notes on Individual Taxa of South Western Australia Centrolepidaceae. Key: Habit, habitat, flowering times (numerical months, eg: 9 = September), Dichogamy in production of male or female flowers, breeding system and in brackets location of populations studied.

***Aphelia cyperoides* R.Br.**

Tufted annual inflorescences exceeding leaves (produces populations with almost sessile inflorescences on the inland margins of range), damplands, swampy open areas, granite moss swards, proterogynous to homogamous, 9–11, self fertile (Scott River, Ruabon, Bullsbrook).

***Brizula muelleri* Hieron**

Tufted annual inflorescences often barely exceeding leaves, damplands, granite moss swards, 8–10, protandrous, self-fertile (Dwellingup, West Cape Howe).

***Brizula drummondii* Hieron**

Tufted annual inflorescences erect, exceeding leaves, usually emergent aquatic in vernal pools, protandrous, 10–11, self-fertile (Ellen Brook, Brixton Street).

***Brizula nutans* (J.D. Hook. ex Benth.) A.W. Hill**

Tufted annual inflorescences exceeding leaves, pendant, damplands, vernal pools, granite moss swards, protandrous, 8–10.

***Centrolepis alcyroides* (Nees) Walp.**

Tufted annual inflorescences exceeding leaves, vernal pools, edges swamps, granite moss swards, proterogynous to homogamous, 9–10.

***Centrolepis aristata* (R. Br.) Roem. et Schult.**

Tufted annual inflorescences exceeding leaves (produces populations with almost sessile inflorescences on the inland margins of range), damplands (sandgrey, laterite, peaty sand, loam clay); granite moss swards, 8–11, proterogynous to homogamous, self-fertile (Ruabon, Bullsbrook).

***Centrolepis caespitosa* D.A. Cooke**

Densely tufted annual, inflorescences not exceeding leaves, vernal pools, 10–11.

Centrolepis cephaliformis* F.M. Reader subsp. *cephaliformis

Densely tufted annual, inflorescences not exceeding leaves, damplands, edges saline lakes, creeklines, granite moss swards, clay pans, 8–11, proterogynous to homogamous, self fertile (Quairading).

***Centrolepis cephaliformis* F.M. Reader subsp. *murrayi* (J.M. Black) D.A. Cooke**

Densely tufted annual, inflorescences not exceeding leaves, damplands, edges saline lakes, granite moss swards, 8–11.

***Centrolepis drummondiana* (Nees) Walp.**

Tufted annual inflorescences exceeding leaves, sandy soils, damplands, swamp edges, granite moss swards, 9–11, inflorescence length variable, proterogynous to homogamous, self-fertile (Kings Park, Ruabon).

***Centrolepis cremica* D.A. Cooke**

Densely tufted annual inflorescence just exceeding leaves, edges saline lakes, watercourses, claypans, edges granite rocks, 9–11, inflorescence length variable, proterogynous to homogamous, self fertile (Goongarrie Station).

Centrolepis fascicularis Labill.

Perennial cushion forming herb, inflorescence-exceeding leaves, permanently wet swamps, creeklines, proterogynous to homogamous, 11-1.

Centrolepis glabra (F.Muell. ex Sond.) Hieron

Tufted annual inflorescences exceeding leaves, vernal pools, swamp edges, 9-11, inflorescence length variable, proterogynous to homogamous, self-fertile (Ellen Brook, Austin Bay).

Centrolepis humillima F.Muell. ex Benth.

Densely tufted annual, inflorescences not exceeding leaves, edges saline lakes, creeklines, granite moss swards, clay pans, 8-11, proterogynous to homogamous, self fertile (Cannington).

Centrolepis inconspicua W.V. Fitzgerald

Minute annual, inflorescences not exceeding leaves, Vernal pools, moss swards, 9-10, proterogynous to homogamous, self-fertile (Cannington).

Centrolepis mutica (R.Br.) Hieron.

Tufted annual inflorescences exceeding leaves, vernal pools, swamp edges, 10-12, proterogynous to homogamous, self fertile (Capel, Tuart Forest).

Centrolepis pilosa Hieron

Tufted annual inflorescences exceeding leaves, damplands, granite moss swards, 9-11, inflorescence length variable, proterogynous to homogamous, self-fertile (Stirling Range).

Centrolepis polygyna (R.Br.) Hieron

Tufted annual inflorescences exceeding leaves, damplands, swamp edges, saline lakes, granite moss swards, 8-11, inflorescence length highly variable (contains numerous races), proterogynous to homogamous, self-fertile (Austin Bay, William Bay, Cape Leeuwin).

Centrolepis strigosa (R. Br.) Roem. et Scultes subsp. *strigosa*

Tufted annual inflorescences exceeding leaves, damplands, swamp edges, 9-11, inflorescence length variable, slightly proterogynous to homogamous, self-fertile (West Cape Howe).

Centrolepis strigosa subsp. *rupestris* D.A.Cooke

Tufted annual inflorescences exceeding leaves, granite moss swards, 8-10, inflorescence length variable, proterogynous to homogamous, self-fertile (Queen Victoria Rocks).

which has many localised endemics.

Taxon diversity of the Centrolepidaceae (Figure 1) is greatest in the higher rainfall areas of temperate Western Australia. This pattern is very different to the Restionaceae,

which is species rich on the southern sandplains and to a lesser extent on the northern sandplains (Keighery 1984). The other major Monocotyledon and Dicotyledon families display similar trends to the Restionaceae.

Members of the Juncaginaceae (*Triglochin*, 17 species in Western Australia) display an almost identical pattern to the Centrolepidaceae. These are also tiny annual, wind pollinated, self-fertile herbs occupying wet microsites (Keighery 1975).

BIOLOGY

Information on the biology of individual taxa is summarised in Table 1. Authorities for all taxa are given there.

Life Form and Longevity

Western Australian members of the family are all annuals with the exception of one *Centrolepis fascicularis*. This species only occurs in the wettest part of southern Western Australia, the Warren Bioregion, in permanently wet sites under tall shrubs and trees, a micro-site and region which has a low diversity of Centrolepidaceae (Fig. 1).

Habitat

Unlike the Hydatellaceae, whose members are strictly aquatic growing submerged in vernal pools and ponds on granite rocks, the Centrolepidaceae also occur in seasonally moist microhabitats. The only members that are often emergent aquatics in shallow water claypans are *Brizula drummondii*, *Centrolepis alepyroides*, *C. caespitosa*, *C. fascicularis* and *C. glabra*, however, these all also occupy granite rock pools and moss swards which are widespread in temperate

Western Australia. Other members occupy seasonally moist habitats on a wide range of soil types and vegetation types (except closed forest).

Even when these sites are in saline lakes, the root zone of these minute annuals is in a layer of fresh water that has fallen as rain. Some species, such as *C. polygyna* are able to tolerate brackish conditions, especially late in the growing season or on granite rocks in the splash zone of the sea. All members of the Hydatellaceae were thought to be fresh water aquatics, usually of vernal or granite rock pools. However, recently a taxon allied to *Hydatella dioica* has been discovered which grows as a submerged aquatic in saline pools on the eastern side of the Harvey Inlet (Gibson *et al.* 1995).

Flowering Times and Pollination

No previous data has been published on the pollination biology of any member of the family. All members are wind pollinated; inflorescences are generally produced well above the leaves with feathery stigmas and anthers containing dry pollen displayed to aid distribution by the wind (Figures 3, 4 and 5). Most taxa of the family occur in open habitats (claypans, moss swards, salt lakes) where wind movement can readily transport pollen between plants in the usually dense populations that these minute annuals form. All members of the Hydatellaceae in Western

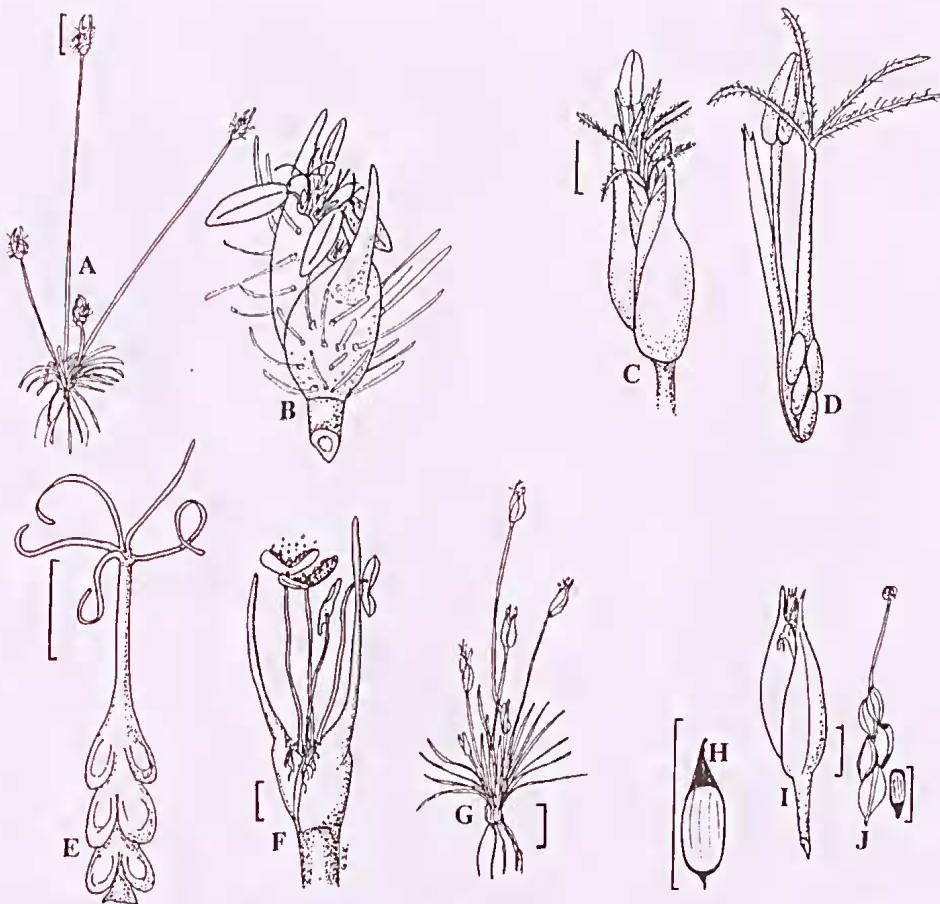


Figure 3. Inflorescences, flowers, fruits and Seeds of *Centrolepis* species. A, Whole plant of *C. pilosa*. B, Inflorescence of *C. pilosa*. C, Female flower of *C. pilosa*. D, Inflorescence of *C. drummondiana*. E, Male and female flowers of *C. drummondiana*. F, Inflorescence of *C. aristata* at pollen dispersal. G, Whole plant of *C. drummondiana*. H, Seed head of *C. drummondiana*. I/J, Seed of *C. drummondiana*. Scale bar=1 mm

Australia are also adapted for wind pollination producing emergent inflorescences with aerially dispersed pollen.

All temperate annual taxa of Centrolepidaceae germinate with the onset of the winter rains (April/May), grow during winter

and early spring (May/September) and flower in spring (August/November).

Breeding Systems

Fifteen taxa have been examined at Kings Park from the genera *Aphelia*, *Brizula* and *Centrolepis*.

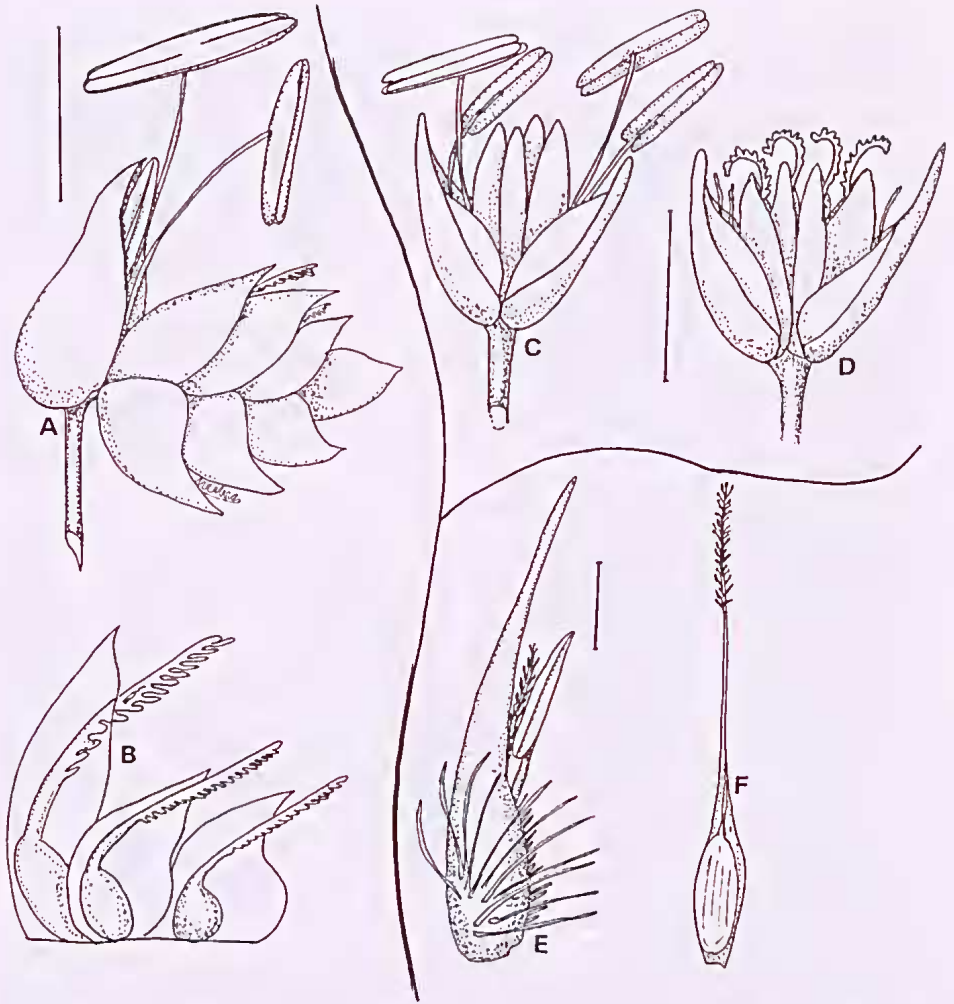


Figure 4. Inflorescences, flowers, fruits and Seeds of *Aphelia* and *Brizula*. A, Inflorescence of *Brizula drummondii*. B, Female flowers of *Brizula drummondii*. C, Inflorescence of *Brizula muelleri* at male stage. D, Inflorescence of *Brizula muelleri* at female stage. E, Single bract of *Aphelia cyperoides* showing male and female flower. F, Single female flower of *Aphelia cyperoides*. Scale bar=1 mm

All were self-fertile although all species display adaptations for outcrossing. This is demonstrated by most taxa occurring in very dense local populations in open habitats, the inflorescence borne

on an elongated scape, often with considerable dichogamy in the presentation of the male and female flowers (Figures 3 and 4). However, there is considerable overlap between inflorescences

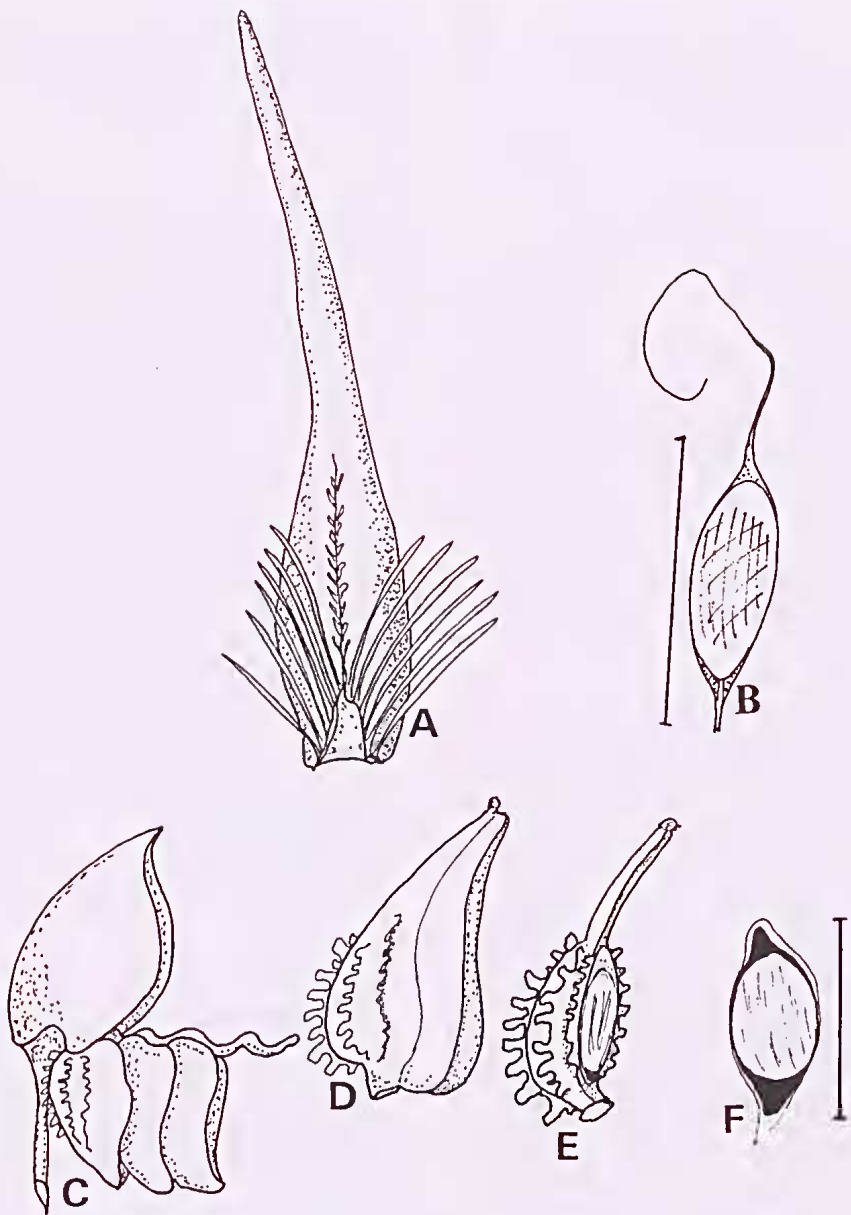


Figure 5. Fruits of *Aphelia* and *Brizula*. A, Single fruit of *Aphelia cyperoides*. B, Seed of *Aphelia cyperoides*. C, Seeding inflorescence of *Brizula drummondii*. D, Single fruit of *Brizula drummondii*. E, Single fruit of *Brizula drummondii* after membranous wing has been lost. F, Seed of *Brizula drummondii*. Scale bar=1 mm

and flower heads in the inflorescence allowing self-pollination to occur.

Most species of Centrolepidaceae have a mixed mating system, with variable levels of inbreeding. Eight taxa have races with sessile inflorescences suggesting higher levels of inbreeding and lower dispersal rates occur in these populations. These populations breed true from seed, suggesting that as in the Juncaginaceae that numerous morphological races occur in these nominally widespread species.

Polyploidy is also common in the family, but only a few counts are currently available (Keighery, unpub. data).

The Hydatellaceae with potentially two dioecious taxa and other species with separate male and female inflorescences are generally highly outbreeding. However, Cooke (1983) noted that the Tasmanian *Hydatella filamentosa* grows completely submerged and that the method of pollination of the family was uncertain but pollen may be transported by water. It may also be that this species like *H. inconspicua* from New Zealand is apomictic (Edgar 1966). In Western Australia all members of this genus need to be cultivated to ascertain if apomixis is present.

The related family Restionaceae is largely dioecious, hence outbreeding but there are also many taxa that have vegetative

reproduction, which is of course not present in the annual taxa of the Centrolepidaceae or Hydatellaceae.

Dispersal

Members of the Centrolepidaceae have a wide variety of dispersal mechanisms. Both *Aphelia* and *Brizula* have fruits that dehisce enclosed by an inflorescence bract. *Aphelia cyperoides* has epizoochorous fruits (Figure 5A), while most *Brizula* species (Figure 4C-E) have fruits that fall directly onto the soil protected by the bracts. Many *Centrolepis* species retain their seeds inside the inflorescence bracts (Figure 3, J-1) for most of summer, protecting the seed from the heat of the surface soil. The inflorescence disintegrates with the first winter rains.

In those species with sessile inflorescences (*C. humillima* and *C. caespitosa*) seed is retained inside the plant, where it germinates in winter or the whole plant is dispersed as tumbleweed. This also occurs in the sessile forms of *Aphelia cyperoides*, *Centrolepis eremica* and *C. polygyna*. This is probably an adaptation to the extremely localised environments these taxa occur in, especially in the arid zone.

The Genera *Aphelia* and *Brizula*

The genera *Aphelia* and *Brizula* are closely related and *Brizula* has been reduced to a synonym of *Aphelia* by a number of reviewers,

Bentham (1878) and Cooke (1995). However, the inflorescence structure of these two groups is so very different (Figure 4). In *Brizula* the male florets are grouped inside a single (or rarely two) large bract at the base of the inflorescence with only female flowers in the distal bracts. Whereas in *Aphelia* the solitary male and female florets occur in each bract of the inflorescence and there is no large basal bract. The stigmas also appear to have very different morphologies (Figure 4, B, D and F) between the two genera.

These inflorescence differences are normally cited as the key differences by those reviewers that separate the genera (Dahlgren and Clifford 1982, Dahlgren *et al.* 1985, Hamann 1975). Based on their reduced structure, yet the major differences in inflorescence structure, I feel that the two genera should be retained until a phylogenetic study is completed.

CONCLUSION

The Centrolepidaceae by reducing their size and generation time have successfully colonised the Mediterranean and winter rainfall arid region of Western Australia, despite being essentially wetland plants. They are modally outbreeding, with high levels of polyploidy and numerous local biotypes rather than localised species.

Their biology contrasts strongly with the Hydatellaceae which are

still true aquatics and the Restionaceae, which are perennial obligate outbreeders, with vegetative reproduction and numerous localised species.

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